

The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process

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Abstract. Woodland (Plethodontid) salamanders are the most abundant vertebrates in North American forests, functioning as predators on invertebrates and prey for higher trophic levels. We investigated the role of *Ensatina eschscholtzii* in regulating invertebrate numbers and leaf litter retention in a northern California forest. Our objective was to examine how salamander predation on invertebrates affects leaf litter retention and the amount available for soil-building and carbon capture at the litter-soil interface. We used field enclosures to quantify the effects of *Ensatina* on invertebrates and litter retention over two wet seasons, using moisture as a covariate. In the first year *Ensatina* reduced Coleoptera (beetles) and Diptera (flies) larvae >2 mm, adult Coleoptera, Collembola (springtails), and Formicidae (ants), and increased Oribatid mites, larvae <2 mm (Diptera and Coleoptera), Diplopoda (millipedes), and Aranea (spiders) <2 mm by reducing their competitors and predators. A single *Ensatina* in a 1.5m² enclosure increased litter retention by 13.3% ± 3.6% (mean ± SE) compared to controls, facilitating the capture of 200 kg/ha of carbon. At a similar density range-wide this would equate to 72.3 metric tons/yr of carbon in one season potentially sequestered in forest soil rather than entering the atmosphere. In the second year invertebrate densities doubled in response to early rains such that while salamanders reduced the numbers of the same taxa, effect sizes were lower compared to year one, producing biological effects that failed to achieve statistical significance. However, three taxa did significantly increase in year two (Annelida [worms], Psocoptera [barklice], and Chelonethida [pseudoscorpions]). Litter retention in year two was greater on treatment plots by 5.6% ± 4.6%; however, high variability across plots precluded statistical significance. *Ensatina* suppressed some invertebrate taxa, released others, increased leaf litter retention, and facilitated greater carbon capture in both years; however, the strength of the effects were modulated by the bottom-up effects of the timing and amount of precipitation in year two.

Key words: ecological service; *Ensatina eschscholtzii*; humification; invertebrate predation; leaf litter retention; northern California; Plethodontidae; trophic relationships; woodland salamander.

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INTRODUCTION

Estes et al. (2011) described the negative consequences of trophic cascades to vital ecolog-

ical processes in Earth's ecosystems due to the loss of apex predators, illustrating the pervasive nature of these losses with a quote from Dan Janzen "... What escapes the eye ... is a much more insidious

kind of extinction: the extinction of ecological interactions” (Janzen 1974). Here we present evidence for an ecological interaction that has gone largely unnoticed, yet has implications for the global carbon cycle. Apex predators are typically thought of as large carnivores in top trophic positions, however, this concept is relative and context dependent (Ritchie and Johnson 2009). In North America’s temperate forests the top predator in food web processes at the forest floor/belowground interface are woodland salamanders (family Plethodontidae) that prey on the numerous invertebrates that initiate the transformation of biomass (i.e., leaf litter, downed wood) into decomposition pathways that direct carbon in this biomass into soil-building or release it as CO₂ and CH₄ (Bardgett and Wardle 2010: Fig. 3.21).

Woodland salamanders, by virtue of their enormous numbers (2950 to 18,000/ ha [Burton and Likens 1975a, Welsh and Lind 1992, Petranksa and Murray 2001, Peterman et al. 2008]), and highly efficient conversion of invertebrate to vertebrate biomass (Pough 1983), are ecologically dominant taxa in nutrient cycling and energy flow in North American forests (Burton and Likens 1975b, Davic and Welsh 2004). It bears noting that what little is known about the ecological roles of woodland salamanders comes primarily from temperate forests, however, over evolutionary time an extensive radiation of these direct-developing (i.e., not requiring water for early life stages) salamanders has extended into the neo-tropics (Wiens et al. 2007), where their trophic roles are mostly undocumented but likely nearly identical to those of temperate species.

Of equal relevance is the fact that in both new and old world tropics, similar ecological niches are occupied by a large, diverse, and highly abundant fauna consisting of many hundreds of species of litter-dwelling frogs (Duellman 1999) and lizards (McDiarmid 2012). Despite their overwhelming numerical dominance among vertebrates in these ecosystems, the roles of woodland salamanders and other litter-dwelling herpetofauna in trophic processes at the above-ground-belowground interface in forests throughout the world are poorly known (but see Wyman 1998, Beard et al. 2003, Walton 2013). Furthermore, the role of litter herpetofauna in carbon pathways that derive from the breakdown and assimilation of litter and woody debris

has been ignored in recent research on carbon pathways (e.g., Beedlow et al. 2004, Kuzyakov 2011, Sayer et al. 2011, Post et al. 2012). Understanding how litter herpetofauna affect decomposition and assimilation pathways of forest litter, augmenting the soil-building process where carbon is captured in forest soil (i.e., humification: Prescott [2010]) is critical missing information. Their huge numbers and trophic roles influence the capacity of forests to capture and store C rather than release CO₂ or CH₄, a critical ecological function that contributes to the amelioration of global warming (Beedlow et al. 2004, Luyssaert et al. 2008, Hudiburg et al. 2009). The need to understand and manage forests to protect and enhance these trophic linkages is urgent given the negative impacts of global warming on these faunas (e.g., Whitfield et al. 2007, Milanovich et al. 2010, Sinervo et al. 2010, Caruso and Lips 2013), impacting a critical ecological service (Cimon-Morin et al. 2013) and compromising the integrity of Earth’s forest ecosystems (IPCC 2014).

Evidence that woodland salamanders influence the forest carbon cycle was first presented by Wyman (1998), who examined the role of red-backed salamanders (*Plethodon cinereus*) in deciduous forest in New York. Wyman (1998), documenting a strong top-down effect on invertebrates that reduced leaf litter disarticulation, slowed decomposition, and resulted in 11–17% more leaf litter on treatment plots compared to controls. These differences resulted in an estimated 261–476 kg of C/ha not released into the atmosphere (Wyman 1998:648). In a similar experiment in the mid-west, Walton (2005) found predation by *P. cinereus* on invertebrate assemblages varied greatly depending on the amounts of leaf litter and moisture. Research on the effects of woodland salamanders on detrital food webs has produced a wide range of results from positive (e.g., Davic 1983, Wyman 1998, Rooney et al. 2000), to mixed (e.g., Walton et al. 2006), to no effects (e.g., Walton and Steckler 2005, Homyack et al. 2010) on invertebrate densities and/or leaf litter retention (reviewed by Walton 2013). These highly variable results illustrate the challenge inherent in documenting the intricacies of complex food webs. In attempting to explain these results Walton (2013) noted that similar variability in experimental outcomes has been

observed with the top-down effects of arthropod predators, concluding that it is reasonable to assume that salamander-mediated dynamics, like those of arthropod predators, are likely to "... vary with prevailing environmental conditions" (Walton 2013:128).

Here we report on an experiment to examine the effects of a woodland salamander, *Ensatina* (*Ensatina eschscholtzii*), on invertebrate densities and leaf litter retention in a western temperate forest, the mixed conifer/hardwood forest of northern California, where *Ensatina* is the most abundant resident salamander (Welsh and Lind 1991). We conducted an exploratory experiment to evaluate the following hypotheses: (1) *Ensatina* has top-down effects on the species composition and densities of invertebrates in forest floor litter; (2) leaf litter breakdown is reduced by *Ensatina* predation; and (3) available moisture influences this relationship by affecting invertebrate abundances which in turn affects the amount of litter retained. The confirmation of these hypotheses in conjunction with the fact that 47.5% of leaf litter is carbon (Schlesinger 1991) would provide evidence that *Ensatina* predation can affect the amount of carbon made available to humification and sequestration in forest soils (Prescott 2010).

MATERIALS AND METHODS

Study site

This experiment occurred in the Mattole River watershed of northwestern California near Etersberg (40°6'3.21" N, 123°58'42.31" W), 400 m above sea level on a forested ridge dividing two Mattole tributaries. The forest was dominated by tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), and Douglas-fir (*Pseudotsuga menziesii*), with scattered black oak (*Quercus velutina*) and canyon live-oak (*Quercus chrysolepis*). This mixed forest deposits litter throughout the year, but the greatest volumes occurs late in the dry season when the dominant hardwoods drop their leaves. Summer temperatures often exceed 32°C (90°F); winters are cool with freezing nights and occasional snowfall. Litter at the site consisted primarily of madrone and tanoak. The area receives little precipitation during spring and summer; however, rainfall in fall and winter averages over 2500 mm (100 inches), exceeding

5000 mm (200 inches) in wet years.

Experimental design

To test the effects of *Ensatina* predation on invertebrates we placed single adult male salamanders (3.5–4.5 g) in each of six 1.5-m² field enclosures, paired with a similar number of control enclosures lacking salamanders. These enclosures, arranged in three sets of four 1.5-m² units (Fig. 1), were 30 cm high, set 15 cm deep into the forest floor, and equipped with a 10-cm aluminum lip around all exterior edges to prevent salamander escapes (Fig. 1). Enclosures were open at the top to allow natural rainfall and leaf litter deposition. Each 4-unit enclosure was randomly assigned two treatment and two control units, with no two treatment plots adjacent (=six treatment and six control units). All units were provided with three rough-cut Douglas-fir bark slabs (~45 cm × 15 cm and 5–8 cm high) for cover. The use of field enclosures to study food web dynamics has been criticized because it can confound predator-prey interactions, including predator avoidance, and the influx of prey from neighboring sites (Walton 2005, Walton et al. 2006). To address these issues we equipped the interior walls with hardware cloth windows (6-mm mesh) to allow for arthropod migration between experimental units while preventing salamander movements. All salamanders existing naturally in these enclosures were removed before initiation of the experiment. Salamanders used in the study were released at the site at the end of the experiment.

The experiment was run over four winter months in each of two years (2007–2008 [hereafter 2007] and 2008–2009 [hereafter 2008]). Invertebrate samples were collected in each study unit prior to salamander introductions, and once each 30-d period after introduction. Leaf litter bags of the same tree species composition and weight (3.0 g) were placed in control and treatment units with salamander introductions and removed after 120 days to assess changes in mass. The experiment started 1 November 2007 with the onset of rain when salamanders became present at the surface in the surrounding forest. Treatment plots were populated over three weeks and all salamanders removed by 22 March 2008, 120 days after the last plot was populated. In 2008 rain was delayed and introductions occurring 30



Fig. 1. Experimental enclosures in situ near Ettersburg, California. Each enclosure contained four 1.5-m^2 experimental units. Overall outside dimensions = $3\text{ m} \times 3\text{ m} \times 23\text{ cm}$; interior unit dimensions = $1.5\text{ m} \times 1.5\text{ m} \times 23\text{ cm}$.

December 2008 through 11 January 2009. Salamanders were removed by 15 May 2009, 120 days after the last introduction. Enclosures were relocated in the second year to avoid sampling the same areas in consecutive years. Animal handling methodologies were approved by the Animal Care and Use Committee at Humboldt State University, protocol number 06/07.W.150.A.

Invertebrate samples

Invertebrate samples consisted of five leaf litter cores extracted from each unit in each month, collected with a soup can (486 cm^3) with both ends removed and pushed firmly down through the leaf-litter until contact with mineral soil. Sample locations were determined with a random number generator and a 100-point grid, stratified to encompass three samples along unit

edges and two samples in the interior. Sample locations were not reused. Holes generated from removing litter cores were measured to determine litter depth then collapsed to prevent drying and to minimize disturbance to soil strata. The five core samples from each unit in each time period were combined to create the monthly invertebrate sample for each unit. Sample cores were immediately placed into Ziploc bags and into a cooler to prevent drying or mobile invertebrates from escaping. Samples were kept at 1–5°C until processed within 48 h in Berlese-funnel extractors with vials of 95% ethanol underneath to collect invertebrates. Leaf litter in the core samples were weighed before and after the drying and extraction process, with the five core samples averaged for each unit and time to determine percent moisture which was used as a covariate in the analysis. For statistical analyses invertebrate abundances in each core sample were divided by the dry weight of the litter to correct for variable litter depth, and then combined to generate invertebrate densities (number/g dry leaf litter) for each unit and time period.

In order to evaluate differences between control and treatment plots based on both prey type and prey size, we examined invertebrate samples under a dissecting microscope, identifying them to family, and assigning them to three size classes: <1 mm, between 1 and 2 mm (<2 mm), >2 mm (small, medium, and large, respectively). Invertebrate taxa were also combined into functional groups: decomposers (shredders/grazers), predators, herbivores, and omnivores (ants) (McBrayer and Reichle 1971). Due to low sample sizes, fly and beetle larvae, determined by examining mouth parts to be shredders, were combined into one group (=larvae). Larvae determined to be predators based on mouth morphology were included in predators; these were comprised of immature stages in the orders Coleoptera and Neuroptera. The identification of mites was simplified into two groups: Oribatidae (fully sclerotized) and non-Oribatidae (not or partially sclerotized) mites.

To quantify the daily impacts of salamanders on invertebrate taxa reduced by their predation we multiplied the sample counts for the month of greatest impact by 20 (monthly samples constituted 1/20th of plot area), then divided by salamander/day (e.g., 150 for year one: one

salamander $\times$ five plots $\times$ 30 days) then subtracted treatment from control values to estimate daily consumption of individual salamanders.

Leaf litter bags

The litter matrix at the study site consisted primarily of tanoak and madrone leaves. We populated study units with three mesh bags (3 mm mesh), each containing 3.0 g of leaf litter (equal amounts of madrone and tanoak), made of window screen and open at one end. Leaves, fully intact with no evidence of decomposition were collected from an area approximately 50 m² centered on the location of the experiment, dried in an oven at 93°C for two hours and weighed out to 3.0-g increments. The 36 litter bags were filled and deployed at one time so that the drying and weighing conditions were consistent. Leaf-litter bags were collected at the end of the experiment and re-dried at 93°C for two hours and re-weighed immediately upon drying to ensure the accuracy of dry-weight measurements. The change in weight from the initial 3.0 g to final dry weight was averaged across the 3 litter bags in each plot and used to compare mean leaf litter weights between controls and treatments. Hardwood leaves are composed of approximately 50% carbon by weight (carbon mass = $0.475 \times$ mass of dried leaf [Schlesinger 1991]); we used this value to calculate the amount of leaf litter dry weight that was carbon in order to estimate the amounts retained or lost over the course of the experiment in each year.

Statistical analysis

We used a general linear model (GLM) analysis of variance with repeated measures to test for significant effects of three independent variables (treatment, moisture, month), and their interactions, on each invertebrate group. The analysis was conducted in SAS 9.2 (SAS Institute 2008). A generalized linear model was not used because the over dispersion parameter was too large to be considered a good fit; over dispersion increased consistently with increasing counts. Invertebrate counts were log transformed [$\log(-\text{count} + 1)$] to achieve normality. Residuals were examined to assess the adequacy of transformations; these were approximately normal and relatively constant across the predicted values. The change in dry weight of the leaf litter bags

from start to end were compared for each year using ANOVA in NCSS (Hintze 2001).

Invertebrate samples were treated as repeated measures because they occurred in the same plots monthly in each year of the experiment. Walton (2005) found a significant influence of moisture and litter mass on invertebrate densities, which altered his top-down regulation by salamanders. Consequently, differences in rainfall timing and amounts between the two years made it imperative we analyze data for each year separately. The depths of each litter core and the amount of moisture they contained were highly correlated, requiring us to select one (i.e., moisture) for our analysis. The variable 'month' included all effects other than moisture and control/treatment, including temperature extremes (freezing nights, warm days) and biotic interactions (e.g., invertebrate birth/recruitment, predation, parasitism/disease, and movements).

The response variables used in the GLM analysis were the log transformed densities of each invertebrate taxon (or functional group) per g of dried leaf litter. Invertebrate families commonly consumed by *Ensatina* (Stebbins 1954, Bury and Martin 1973) were broken into separate variables (by size class) to increase the resolution of possible impacts to these groups. Invertebrate families not commonly consumed by *Ensatina* (Stebbins 1954, Bury and Martin 1973) were analyzed as single response variables that included all sizes. Invertebrate families identified as *Ensatina* prey, but that contained insufficient data for separate analyses by size class were also treated as single response variables that included all sizes. With the functional groups, only decomposers contained a sufficient sample to enable an analysis by size class. Individual taxa that comprised <0.1% of the total sample were eliminated prior to the analysis (see Supplement). The GLM terms for each response variable are as follows:

$$\begin{aligned} &\log(\text{count} + 1) \\ &= \text{intercept} + \text{month} + \text{control}_{\text{trt}} \\ &\quad + \text{percent moisture} + \text{month} \times \text{control}_{\text{trt}} \\ &\quad + \text{month} \times \text{percent moisture} \\ &\quad + \text{percent moisture} \times \text{control}_{\text{trt}} \\ &\quad + \text{percent moisture} \times \text{month} \\ &\quad \times \text{control}_{\text{trt}} + r + e. \end{aligned}$$

The individual 1.5-m² plot was the unit of analysis; 12 plots were divided equally between control and treatment ("trt"). One treatment and one control plot were omitted from the analysis in 2007 due to an escaped salamander.

Strict adherence to standard Type I error reduction methods (e.g., Bonferroni corrections) impose a heavy and inappropriate burden on community-level studies because the ability to detect biologically relevant effects declines as the number of taxa analyzed increases (Moran 2003). However, an even more fundamental consideration is whether adjustments in the significance level are even appropriate in some cases of multiple testing (Roback and Askins 2005, Waite and Campbell 2006). Because we applied the GLM once to each independent invertebrate group in each year in an exploratory (not confirmatory) analysis, we considered adjustments for multiple comparisons unnecessary and inappropriate (Roback and Askins 2005, Waite and Campbell 2006). The alpha level for all tests was $p \leq 0.10$: appropriate for exploratory ecological studies (Schrader-Frechette and McCoy 1993).

RESULTS

Invertebrates

In the first year (2007) samples from 10 plots yielded 14,408 invertebrates from 38 families. In the second year (2008) samples from 12 plots yielded 32,721 invertebrates from 48 families (Table 1) (see Supplement). Invertebrates were approximately half as abundant in leaf litter samples in 2007 compared to 2008; however, the relative composition of functional groups was nearly identical in the two years (Table 1). The majority of invertebrates were decomposers (95%), with mites nearly three times as dense (~60%) as springtails (~20%); all other decomposers comprised less than 10% of the total; ratios that were consistent in both years (Table 1). Herbivores, predators, and omnivores (ants) together comprised less than 5% of samples in both years. Rainfall during the experiment was 1128.7 mm (2007–2008) and 1075.4 mm (2008–2009), respectively, with most falling at the beginning of the study in year two in contrast with year one. Rain amounts tracked closely with changes in invertebrate abundances in both years (Fig. 2).

Table 1. Abundances (and percentages of total) of common invertebrate taxa on experimental plots in the Mattole watershed of northern California in 2007 and 2008.

Invertebrate taxa	2007		2008	
	Abundance	Percentage of total	Abundance	Percentage of total
Springtails	3304	23.0	7269	22.2
Mites	9187	63.8	22116	67.6
Other decomposers	1318	9.1	1828	5.6
Herbivores	28	0.2	360	1.1
Predators	289	2.0	580	1.8
Ants	282	2.0	568	1.7
Total	14,408	100	32,721	100

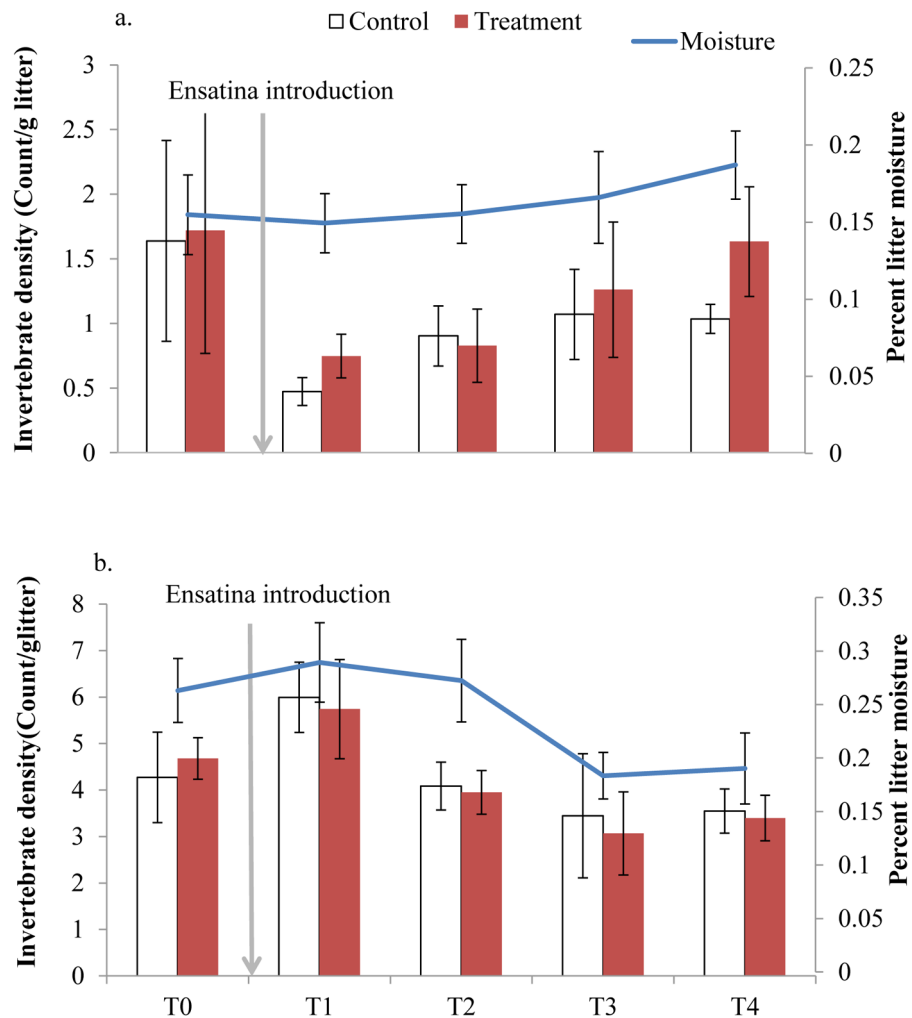


Fig. 2. Mean density of all invertebrates from (a) 2007 and (b) 2008, sampled at five monthly intervals on control and treatment plots. The blue line represents the percent litter moisture in 2007–2008. Error bars are ± 1 SE. T0–T4 = 2007: November–March; 2008: January–May.

Table 2. Analysis of the effects of salamander predation (Control_Treatment) moisture, month, and the interaction of month $\times$ moisture, on invertebrate functional groups by size class in two years using a general linear model. Data analyzed separately by group, size, and year. Year 1, $df = 190$; Year 2, $df = 230$. Statistical significance (in boldface) at $\alpha = 0.1$.

Group/size	Year	Control_Treatment		Moisture		Month		Month $\times$ Moisture		Moisture Response
		F	P	F	P	F	P	F	P	
Decomposers										
< 1 mm	1	0.0001	0.99	10.31	0.002	1.91	0.11	2.09	0.083	+
< 2 mm	1	0.87	0.35	9.91	0.002	1.46	0.22	1.50	0.20	+
> 2 mm	1	0.54	0.46	1.22	0.27	0.86	0.49	0.85	0.49	
< 1 mm	2	0.79	0.37	20.94	<0.0001	5.01	0.001	5.56	0.0003	+
< 2 mm	2	0.64	0.42	3.92	0.049	3.18	0.014	4.41	0.002	+
> 2 mm	2	0.82	0.37	22.66	<0.0001	2.56	0.039	2.37	0.053	+
Ants										
All sizes	1	0.15	0.70	14.24	0.0002	0.52	0.72	1.46	0.21	
All sizes	2	0.17	0.68	0.06	0.80	1.36	0.25	0.43	0.79	
Predators										
All sizes	1	0.93	0.33	3.64	0.058	1.28	0.28	1.08	0.37	
All sizes	2	0.47	0.49	0.52	0.47	1.72	0.14	2.02	0.092	+
Herbivores										
All sizes	1	0.37	0.54	2.49	0.12	0.24	0.91	0.38	0.82	
All sizes	2	0.27	0.60	0.07	0.79	9.81	<0.0001	1.43	0.23	+
All inverts										
All sizes	1	0.03	0.87	17.48	<0.0001	2.09	0.08	2.23	0.07	+
All sizes	2	0.73	0.39	18.52	<0.0001	4.84	0.0009	6.06	0.0001	+

In both years invertebrate densities were similar between controls and treatments prior to salamander introductions (2007: $t = 0.12$, $df = 190$, $p = 0.90$; 2008: $t = -0.05$, $df = 230$, $p = 0.96$) (Fig. 2), and significantly influenced by moisture (2007: $F = 17.48$, $df = 190$, $p < 0.0001$; 2008: $F = 18.52$, $df = 230$, $p < 0.0001$), month (2007: $F = 2.09$, $df = 190$, $p = 0.08$; 2008: $F = 4.84$, $df = 230$, $p < 0.0009$) and their interaction (2007: $F = 2.23$, $df = 190$, $p = 0.07$; 2008: $F = 6.06$, $df = 230$, $p = 0.0001$) (Table 2). While densities appeared to fluctuate with available moisture in both years, patterns differed between years (Fig. 2). We found no significant effect of *Ensatina* on total invertebrate densities in either year (2007: $F = 0.03$, $df = 190$, $p = 0.87$; 2008: $F = 0.73$, $df = 230$, $p = 0.39$) (Table 2); however, there were significant effects on densities of specific taxa (Table 3).

Effects of *Ensatina* on individual invertebrate taxa

Densities of eight invertebrate groups were significantly affected by *Ensatina* in 2007; four increased and four decreased (Table 3). In 2007 the densities of Diptera and Coleoptera larvae > 2 mm ($F = 2.79$, $df = 190$, $p = 0.096$), Entomobryidae springtails < 2 mm ($F = 3.32$, $df = 190$, $p = 0.070$), and adult Coleoptera < 2 mm ($F = 6.39$, $df = 190$, $p = 0.012$) all declined significantly on

Ensatina plots in the first and second month following introductions (December and January) (Figs. 3a, 4a, c) (Table 3). Two groups that declined on treatments in 2007 (larvae > 2 mm and Entomobryidae springtails < 2 mm) rebounded to densities higher than on controls following the initial declines (Figs. 3a, 4a). The density of ants was low on all plots through the first three months of 2007, however they decreased significantly on treatments in March (Fig. 3b), revealing a significant interaction between month, moisture, and treatment ($F = 4.09$, $df = 190$, $p = 0.003$) (Table 3). The density of Oribatidae mites < 1 mm increased significantly on plots with *Ensatina* in December of 2007 after introductions, and again in March (Fig. 5a); with a significant interaction between treatment and month ($F = 2.69$, $df = 190$, $p = 0.032$) (Table 3). In 2007 the densities of larvae < 2 mm were similar between control and treatments in the first month following introductions, but then increased on treatments in January and March ($F = 3.85$, $df = 190$, $p = 0.051$) (Fig. 3c, Table 3). The densities of millipedes were greater on treatments in December, January, and March of 2007 ($F = 2.31$, $df = 190$, $p = 0.059$) (Fig. 5b, Table 3), and spiders < 2 mm were found in higher densities on treatments compared to controls ($F = 2.79$, $df = 190$, $p =$

Table 3. Analysis of the effects of salamander predation (Control_Treatment) and their interactions with moisture and time interval (month) on invertebrate taxa in two years using a general linear model. Data were analyzed separately by taxon, size class, and year. Year 1, $df = 190$; Year 2, $df = 230$. Statistical significance (in boldface) at $\alpha = 0.1$.

Taxa/size	Year	Control_Treatment		Moisture $\times$ Treatment		Month $\times$ Treatment		Month $\times$ Moisture $\times$ Treatment		Treatment Response
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Springtails†										
< 2 mm	1	3.32	0.070	3.52	0.062	0.49	0.74	1.87	0.11	—
< 2 mm	2	0.23	0.63	0.93	0.34	1.93	0.11	1.87	0.12	
Adult beetles										
< 2 mm	1	6.39	0.012	5.27	0.023	1.31	0.27	1.12	0.35	—
< 2 mm	2	1.96	0.16	0.94	0.33	1.62	0.17	1.64	0.16	
Larvae‡										
< 2 mm	1	3.85	0.051	2.12	0.15	1.16	0.33	0.93	0.45	+
> 2 mm	1	2.79	0.096	1.28	0.26	1.02	0.39	1.08	0.37	—
< 2 mm	2	0.11	0.75	0.06	0.81	0.26	0.91	0.13	0.97	
> 2 mm	2	0.24	0.62	0.15	0.69	1.48	0.21	1.36	0.25	
Mite-Oribatid										
< 1 mm	1	0.06	0.81	0.003	0.96	2.69	0.032	2.16	0.075	+
< 1 mm	2	1.66	0.19	1.97	0.16	0.15	0.96	0.39	0.82	
Spiders										
< 2 mm	1	2.79	0.097	2.77	0.098	0.61	0.66	0.79	0.53	+
< 2 mm	2	0.02	0.90	0.33	0.57	0.82	0.51	0.72	0.58	
Ants										
All sizes	1	0.15	0.70	0.001	0.97	2.79	0.27	4.09	0.003	—
All sizes	2	0.17	0.68	0.03	0.87	0.75	0.56	0.84	0.51	
Millipedes										
All sizes	1	0.14	0.71	0.51	0.47	2.31	0.059	3.36	0.01	+
All sizes	2	1.34	0.25	0.83	0.36	0.28	0.89	0.41	0.80	
Bark lice										
All sizes	1	0.09	0.76	0.003	0.96	0.16	0.96	0.29	0.89	
All sizes	2	3.04	0.083	2.67	0.10	1.08	0.36	1.07	0.37	+
Worms										
All sizes	1	0.15	0.70	0.006	0.94	0.68	0.60	0.96	0.43	
All sizes	2	1.13	0.29	3.40	0.066	0.30	0.88	0.53	0.71	+
Pseudoscorpion										
All sizes	1	0.53	0.47	0.29	0.59	1.59	0.17	1.09	0.36	
All sizes	2	1.66	0.19	0.52	0.47	1.73	0.14	2.07	0.086	+

† Springtails determined to be members of the family Entomobryidae by examination of morphological features.

‡ Larvae determined to be saprophytic shredders by examination of morphology, include immature stages of: beetles and flies.

0.097) (Fig. 5c); both showed significant interactions with moisture (Table 3).

The daily impact of individual salamanders on invertebrates significantly reduced in year one were as follows: larvae (shredders—immature stages of Diptera and Coleoptera) > 2 mm, two larvae/day (Fig. 3a, December); adult beetles (Coleoptera, mostly family Ptiliidae) < 2 mm, one beetle/day (Fig. 4c, December); springtails (Collembola, Entomobryidae) < 2 mm, 0.5 springtails/day (Fig. 4a, December); ants (Formicidae) all sizes, 20 ants/day (Fig. 3b, March).

In contrast to 2007, only three taxa were significantly affected in 2008, all increasing on treatment plots (Table 3). The densities of two taxa which declined significantly in 2007 showed

a similar trend in 2008, Entomobryidae springtails <2 mm and beetles <2 mm (Fig. 4b, d); however, these differences failed to reach significance in year two (Table 3). The densities of worms (Annelida) ($F = 3.40$, $df = 230$, $p = 0.066$) and barklice (Psocoptera) ($F = 3.04$, $df = 230$, $p = 0.083$) increased significantly on treatments in March and May (Fig. 6a, b); with a significant interaction between treatment and moisture for the worms (Table 3). Pseudoscorpions (Chelonethida) was the third taxon with higher densities on treatments in 2008, increasing in February, and in April and May (Fig. 6c); with a significant interaction between month, moisture, and treatment ($F = 2.07$, $df = 230$, $p = 0.086$) (Table 3).

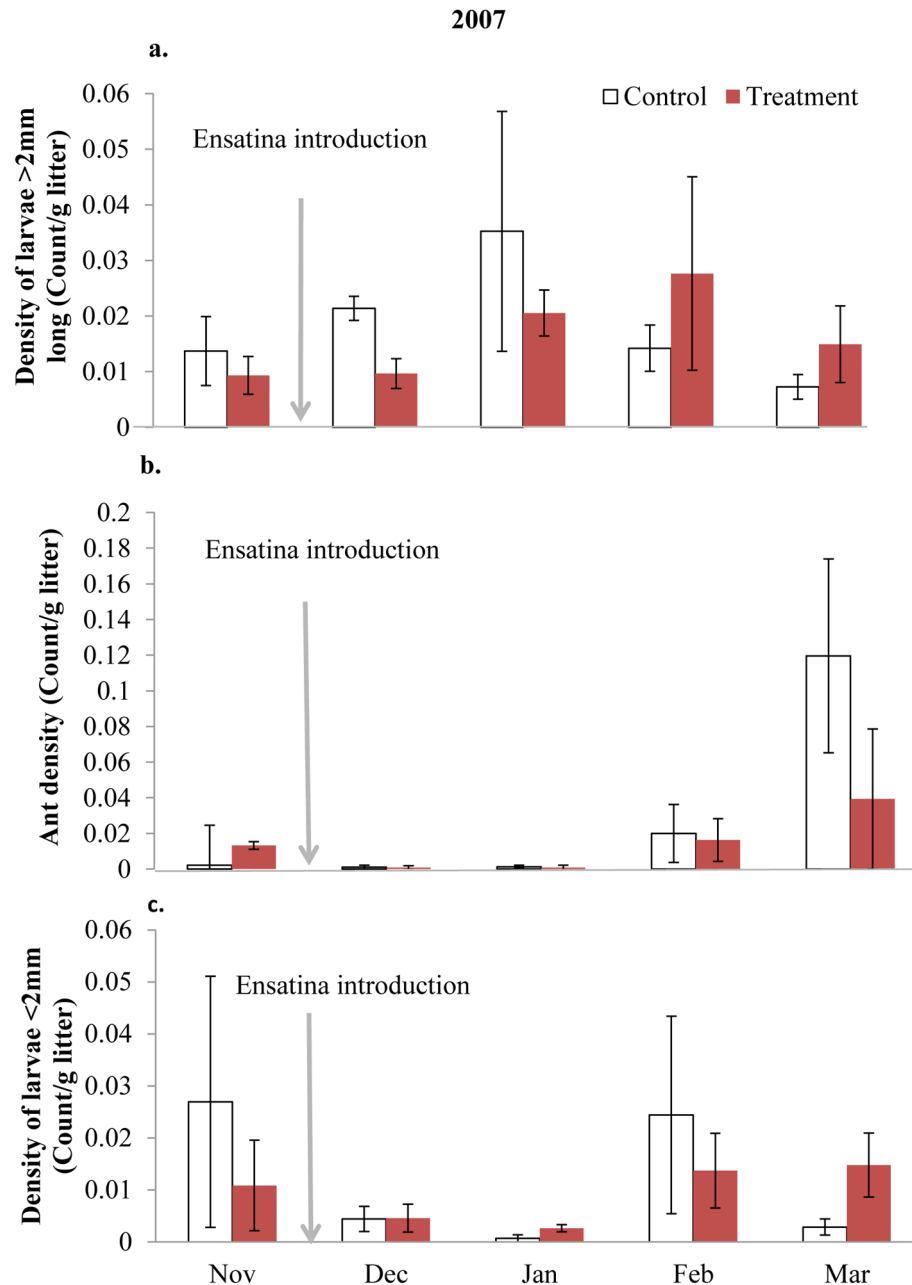


Fig. 3. Mean density of (a) larvae >2 mm, (b) ants, and (c) larvae <2 mm, sampled at five monthly intervals on control and treatment plots in 2007. Error bars are ± 1 SE. $N = 25$.

Leaf litter

In 2007 leaf litter (dry weight) was significantly greater on treatments (2.68 ± 0.03 g [mean $\pm$ SE]) compared with controls (2.34 ± 0.03 g) ($F = -49.16$, $df = 8$, $p = 0.0001$). The retention of leaf-litter (i.e., breakdown reduced) was $13.3\% \pm$

3.6% higher. However, in 2008 the litter mass, while on average $5.6\% \pm 4.6\%$ greater on treatments (2.23 ± 0.13 g), was not significantly different compared to controls (2.06 ± 0.13 g) ($F = -0.94$, $df = 10$, $p = 0.355$). The average retention of litter mass in bags across all plots (treatment

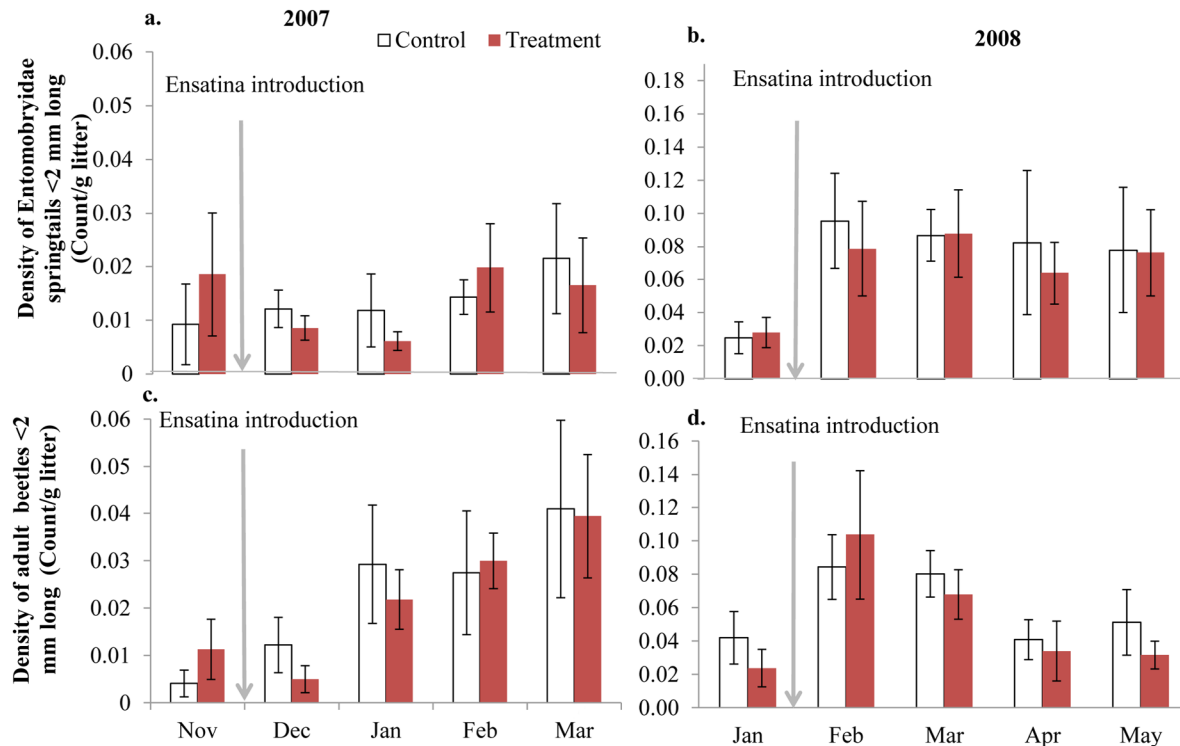


Fig. 4. Mean density of (a) Entomobryidae springtails <2 mm sampled in 2007 and (b) in 2008, and (c) mean densities of beetles <2 mm sampled in 2007 and (d) in 2008; samples were collected at five monthly intervals on control and treatment plots. Error bars are ± 1 SE. $N = 25$ in 2007; $N = 30$ in 2008.

and control) in 2008 (2.14 ± 0.08 g) was significantly less ($F = 10.88$, $df = 1$, $p = 0.004$) than it was in 2007 (2.51 ± 0.08 g); with greater litter breakdown across all plots in the second moister year. On average in 2007 litter bags lost ~ 0.5 g of mass compared to 2008 when the loss averaged ~ 1.0 g.

DISCUSSION

We found that predation by *Ensatina* on two invertebrate functional groups in the litter-to-soil process (grazers [i.e. Entomobryidae springtails, beetles] and shredders [i.e. larvae]) directly influenced the amount of litter breakdown. However, the effect of this top-down predation on the amount of litter retained was influenced by the bottom-up effects of moisture (see also Walton 2005, 2013). The densities of most common *Ensatina* prey taxa (i.e., springtails, spiders, millipedes, beetles, larvae, ants, mites [Stebbins 1954, Bury and Martin 1973, Lynch

1985]) differed significantly on plots with salamanders in the first year. However, in the first two months of the second year, consistent with an initial high pulse of moisture, we sampled roughly twice as many invertebrates compared with year one. This increased invertebrate biomass enhanced litter decomposition, with litter breakdown greater in the second year compared with the first. Consistent with this enhanced litter breakdown, significant direct top-down negative effects of salamanders on specific invertebrates observed in the first year were absent in year two, although we did detect indirect effects where specific taxa increased. While *Ensatina* did not significantly alter total invertebrate density across all time intervals of the experiment, they did alter the densities of specific taxa during discrete intervals, which potentially influenced the pathways of carbon via either decomposition or humification (Prescott 2010).

In the first year both declines and increases (releases due to the elimination of competitors or

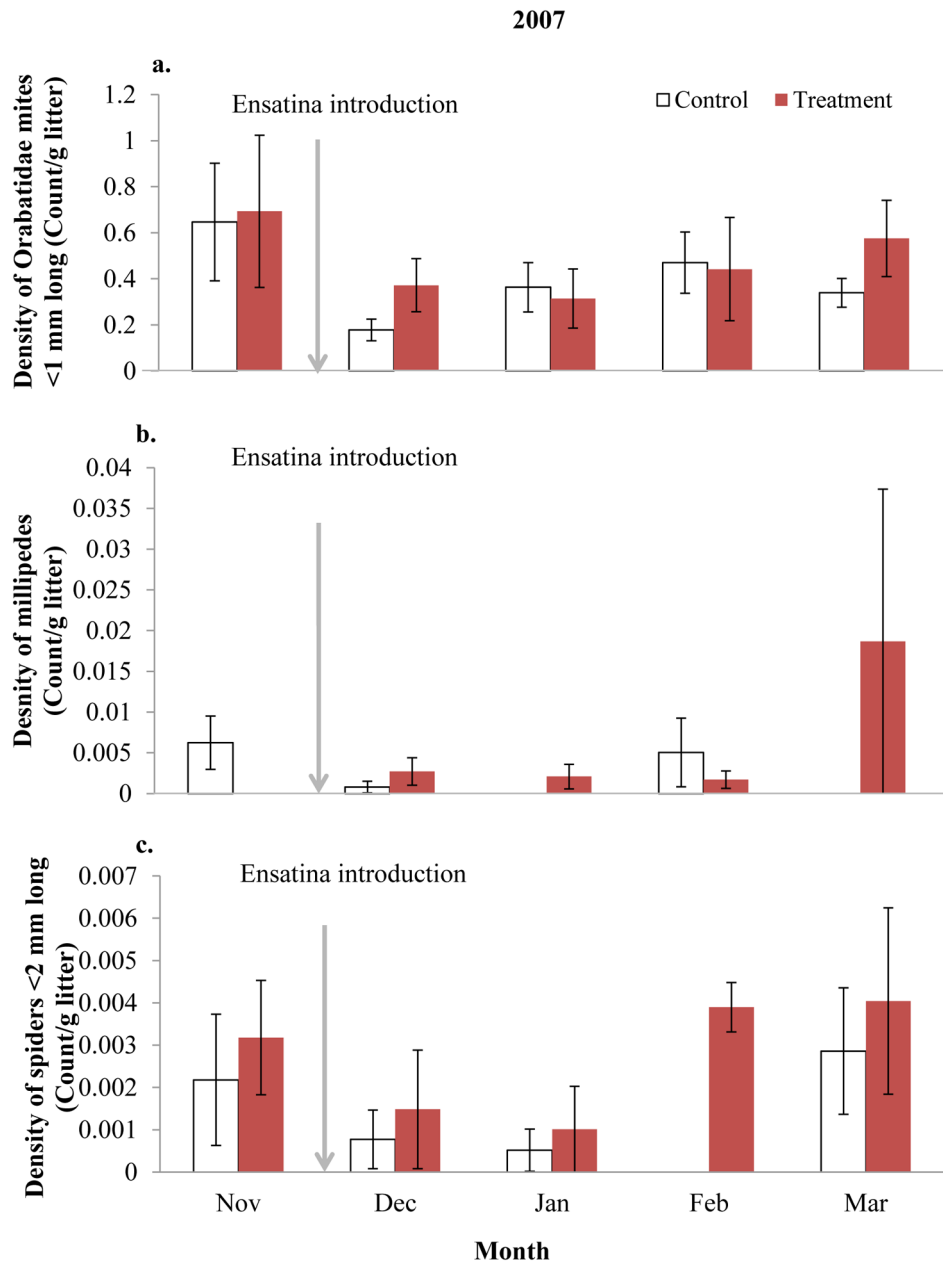


Fig. 5. Mean density of (a) Oribatidae mites <1 mm, (b) millipedes, and (c) spiders <2 mm, sampled at five monthly intervals on control and treatment plots in 2007. Error bars are ± 1 SE. $N = 25$.

predators) of invertebrates due to the presence of *Ensatina* were apparent in the first month after introduction. Densities of two microfloral grazers: Entomobryidae springtails (<2 mm), adult beetles (<2 mm), decreased immediately, while the density of Oribatidae mites <1 mm (microfloral grazers) increased. The removal of these

two larger grazers by *Ensatina* probably opened up resources for the smaller and more numerous mites, allowing their increase (competitive release). A similar relationship was found with *Plethodon cinereus* which decreased abundances of Entomobryidae springtails on salamander plots, resulting in increases in mites and podo-

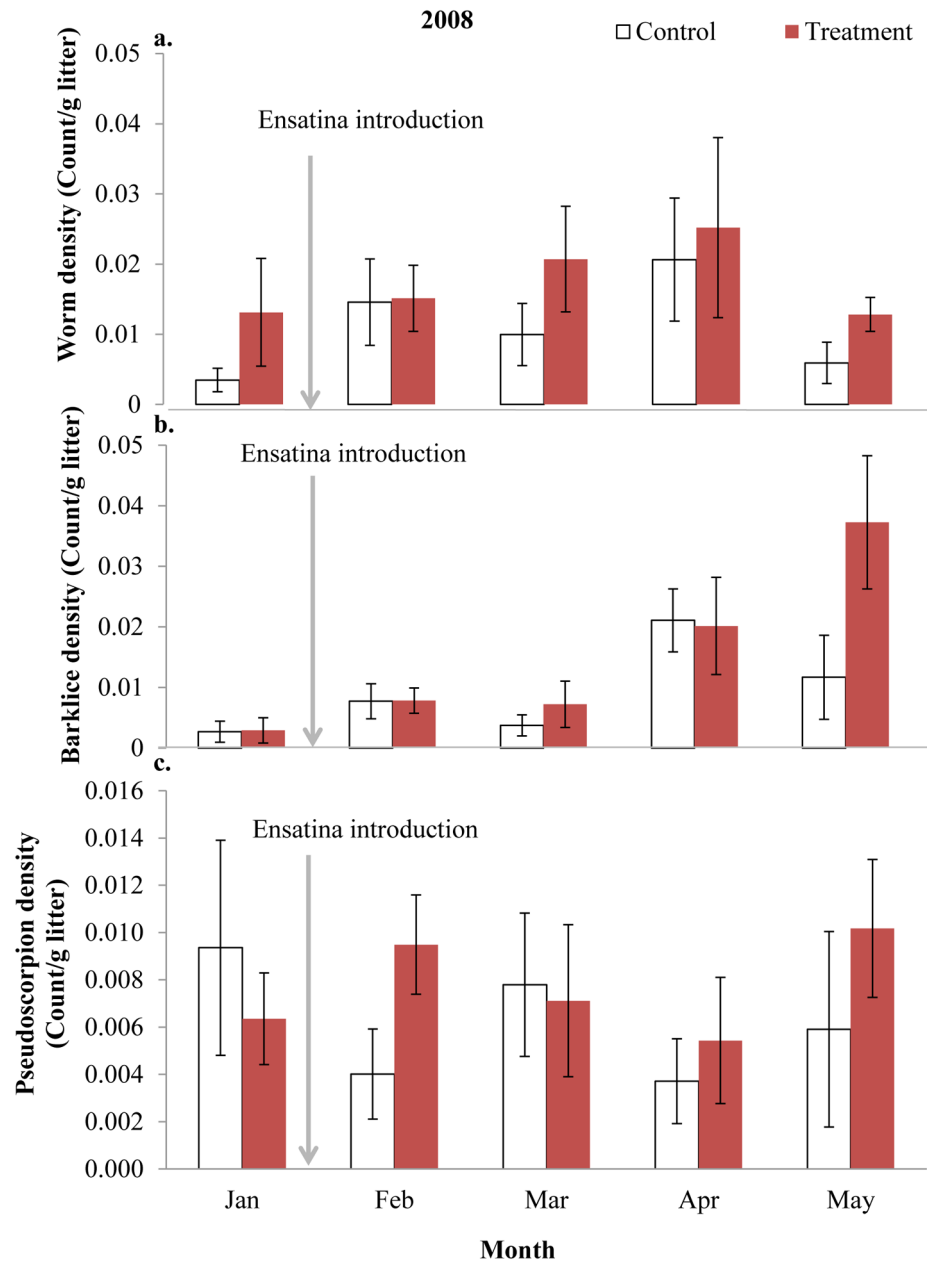


Fig. 6. Mean density of (a) worms (Annelida), (b) barklice (Psocoptera), and (c) pseudoscorpions (Chelonethida), sampled at five monthly intervals on control and treatment plots in 2008. Error bars are ± 1 SE. $N = 30$.

morphic (families Onychiuridae and Hypogasturidae) springtails (Walton and Steckler 2005). Rooney et al. (2000) and Walton et al. (2006) also described releases of podomorphic springtails by *P. cinereus*. In our study, the larger and highly mobile millipedes (a microfloral grazer) also

apparently capitalized on the enhanced availability of microfloral resources by increasing in density on *Ensatina* plots. Larval shredders > 2 mm decreased in the first two months of 2007 on treatment plots, which allowed intermediate larval shredders (< 2 mm) to increase. Concom-

itant with the reduced densities of large larval shredders and microfloral grazers (springtails, beetles) leaf litter retention increased $13.3\% \pm 3.6\%$ on treatments over controls.

The markedly increase in invertebrates early in the second year limited the ability of a single salamander in a 1.5-m^2 plot to consume sufficient numbers to significantly reduce densities. None-the-less salamanders did consume appreciable numbers of Entomobryidae springtails and beetles (Fig. 4b, d), resulting in a competitive release of the small ($<1\text{ mm}$) microfloral grazer barklice (Psocoptera) (Fig. 6b) (see also Christie et al. 2010). By May, barklice were three times more abundant on *Ensatina* plots compared to controls. Walton (2005, 2013) also observed increases in barklice on plots with *P. cinereus*.

Consistent with the early pulse of moisture and higher invertebrate densities in year two, was greater litter breakdown across all plots compared with year one. Regardless, the mean dry weight of litter retained on treatment plots was $5.6\% \pm 4.6\%$ higher than on controls in year two, indicating that *Ensatina* predation, while failing to achieve statistical significance, none-the-less had discernible and biologically relevant effects on the system. In both years we saw *Ensatina* impacts on the same invertebrates (Entomobryidae springtails $<2\text{ mm}$, beetles $<2\text{ mm}$, and larvae $>2\text{ mm}$) in times of less moisture; however, the years differed with the lowest moisture at the beginning of 2007 and at the end of 2008 (Fig. 2). The first two months after salamander introduction in 2007 and the last three of 2008 both coincided with declines in moisture and had fewer invertebrates, which likely limited prey choices as availability declined (Jaeger and Barnard 1981). Walton (2005, 2013) also found the top-down predatory effects on invertebrates to be ameliorated by moisture. The bottom-up effect of moisture on the top-down regulation of invertebrates has been documented with other vertebrate predators (e.g., *Anolis* lizards [Spiller and Schoener 1995]; arboreal birds [Bridgeland et al. 2010]).

Ensatina has the widest gape of western plethodontids, allowing it to consume a variety of prey, with moderate sized adult salamanders (35–49 mm, snout-vent-length) consuming mostly small ($<0.3\text{ mm}^3$) and medium ($<19\text{ mm}^3$) sized invertebrate prey; 45% of their diet by

volume was small and 55% medium, with less than 0.2% of prey greater than 19 mm^3 (Lynch 1985). While we failed to detect significant declines in larger invertebrate predators, possibly due to small sample sizes, we did find evidence of indirect increases to intermediate predators in each year (mesopredator release [Ritchie and Johnson 2009]). On treatment plots the first year we found higher densities of spiders $<2\text{ mm}$, and in the second year higher densities of pseudoscorpions. Spiders are a prey choice of *Ensatina* (Stebbins 1954, Bury and Martin 1973) so predation on larger spiders ($>2\text{ mm}$) may explain increases of both small spiders ($<2\text{ mm}$) and pseudoscorpions (see also Walton 2013).

Plethodontid salamanders are poikilotherms with low energetic requirements and greater efficiencies than endotherms when converting ingested calories into biomass (Burton and Likens 1975b, Pough 1983). Low energetic requirements allow *Ensatina* to include abundant prey even when it may be energetically less profitable (Jaeger and Barnard 1981), providing other nutritional qualities (complimentary amino acids, etc.; Stamps et al. 1981, Mayntz and Toft 2001). These circumstances provide *Ensatina* great flexibility in prey selection in response to varying conditions (i.e., moisture, temperature, prey density). *Ensatina* are sit-and-wait predators that invest little energy in foraging so a majority of the cost is inherent in handling which is related to the percentage of chitin in prey exoskeletons (Jaeger 1990, Diaz and Carrascal 1993). The lowest handling times are associated with soft bodied taxa: true bugs, larvae, flies, and spiders; increased handling occurs with highly chitinized and elongated taxa: crickets, beetles, ants, etc. (Jaeger 1990, Diaz and Carrascal 1993). Large beetles and springtails although common in samples (see Supplement) were not significantly reduced by *Ensatina* compared with the smaller size classes ($<2\text{ mm}$), which were reduced in December and January of 2007. Larvae $>2\text{ mm}$ were also important prey for *Ensatina* during the same period, particularly when prey density was the lowest recorded during our study. This is in contrast to larvae $<2\text{ mm}$ which increased on treatments during this same time.

Temperate invertebrate assemblages are highly

skewed towards smaller species which can provide an abundant prey base for small insectivores (Whittaker 1952, Stamps et al. 1981). Jaeger (1980) confirmed that prey abundance is very rarely limiting for terrestrial salamanders, but may become temporarily unavailable due to low moisture or high temperatures which can threaten salamanders with desiccation, suggesting that moisture availability may have a greater influence on *Ensatina* foraging than prey density, and probably explains their retreat from the surface during the dry season (H. H. Welsh, *unpublished data*). During December and January of 2007, invertebrate densities slowly increased from their low, and *Ensatina* consumed prey in more energetically favorable taxa (larvae >2 mm, Entomobryidae springtails and beetles <2 mm). In contrast, in February of 2007 *Ensatina* did not significantly impact these groups, and as moisture and total invertebrate densities peaked in March they consumed ants (=high chitin).

It may be that relatively limited prey availability in 2007 influenced *Ensatina* to consume more energetically advantageous prey (calories/cost) to maintain a positive energy budget (e.g., Jaeger 1990, Diaz and Carrascal 1993), which may have become less important in February and March as prey became more abundant. Alternatively, but not exclusively, it may be that the consumption of prey under cover objects during periods of relatively low moisture (Jaeger 1980) influenced *Ensatina* to capitalize on particular taxa commonly encountered under cover (beetles, Entomobryidae springtails, larvae). Increased moisture in February and March of year one may have allowed *Ensatina* access beyond cover and to consume a wider variety of prey.

These two phenomena were likely a part of the dynamics of the second year where top-down salamander effects did not significantly decrease densities of invertebrate taxa, and with moisture and invertebrate densities high, there was nothing to limit foraging behavior. Furthermore, the significant indirect effect of *Ensatina*, which increased the density of barklice, occurred first in March and again in May, when moisture and invertebrate density were both most limited in 2008. The early pulse of moisture in the second year may have limited the ability of *Ensatina* to regulate the more abundant invertebrates, limit-

ing their ability to significantly increase leaf litter retention.

Litter herpetofauna, forests, and carbon

Variability across forest litter food webs can be extreme. For example, while Walton's (2013) study and ours are not directly comparable for methodological reasons, they do serve to illuminate regional differences. We sampled 47,129 invertebrates over two years, while Walton reported 23,964 invertebrates over six years; half as many in three times the amount of time. Such differences can have profound impacts on litter dynamics. In the first year of our experiment a single *Ensatina* in a 1.5-m² enclosure increased litter retention by 13% $\pm$ 3.6% compared with controls; capturing an estimated 200 kg/ha more carbon (C). At a similar density across the range of *Ensatina* this would equate to 72.3 metric tons of C retained by this one species in a single season, preventing it from entering the atmosphere. The enormous densities and high species richness of terrestrial salamanders in North American forests (see citations in *Introduction*) signifies the ecological dominance of their predatory role in forest trophic dynamics. Members of the invertebrate shredder guild physically disarticulate organic material such as leaf litter into smaller pieces, which are then processed through their guts, inoculated with microflora, and decomposed (Gist and Crossley 1975). Small decomposers (mites, springtails, and nematodes [i.e. microfauna]) directly mediate decomposition and humification (Prescott 2010) of the litter resource by grazing, spreading propagules, and preying on one other (e.g., Drift and Jansen 1977). These microbial grazers and their predators convert microfloral productivity and waste into invertebrate biomass (McBrayer and Reichle 1971, Singh 1977), transferring energy from forest detritus up the food web, simultaneously recharging soil nutrients, including carbon and nitrogen, in addition to releasing CO₂ and CH₄ via decomposition (De Deyn et al. 2008). Decomposition rates and soil carbon pools however are influenced in many other ways such as by plant trait composition, soil fertility, and abiotic conditions (Bardgett and Wardle 2010: Fig. 3.21). However, sequestering more carbon in forest soils requires diverting more litter into humus through both microbial and chemical reactions

rather than having it decompose (Prescott 2010). Most litter downfall in the Mattole occurs prior to the fall rains, which upon arrival have the effect of cohering pieces of downfall together, creating a ‘wet blanket’ over the previous years’ disarticulated and partially decomposed litter. The litter-to-soil processes re-initiated by fall rains direct the carbon downward under moist anaerobic conditions, primarily into microbial humification rather than further disarticulation and decomposition. Prescott (2010: 145) notes “a substantial portion of litter may be humified under suboptimal conditions (cold temperatures and excessive moisture)”; conditions that are the norm during the Mattole wet season as well as in most cool temperate forest regions of North America. As was evident in our second year results, however, this process can be greatly influenced by bottom-up environmental conditions such as the timing and amount of available moisture.

Soils are globally the third largest active carbon pool after the lithosphere and hydrosphere (storing roughly 2400 Petagrams of carbon in the top 2 m; Eshel et al. 2007); representing the largest terrestrial reservoir of carbon (Hungate et al. 2009). These carbon stocks are greatest in the cool, temperate forests of the northern hemisphere (Houghton 2003), where in North America woodland salamanders are extremely abundant and diverse (Petranka 1998). Our results and others (e.g., Wyman 1998, Walton et al. 2006, 2013) indicate woodland salamanders play an important role in the trophic processes at the leaf litter-soil interface in these temperate forest ecosystems. The vital role of predators in the trophic processes that maintain ecological integrity (i.e., resistance and resilience) has only recently become apparent (Ritchie and Johnson 2009, Estes et al. 2011). Woodland salamanders, and other litter herpetofauna, exert top-down effects on invertebrate assemblages, slowing disarticulation and increasing retention of litter mass; mass that is either captured by newly fallen leaves where it can be sealed in by the next wet season, enhancing humification, or further disarticulated and decomposed. Both of these processes will cycle nutrients and minerals, including carbon, either back into the atmosphere and/or into forest soils. How much each process is influenced by top-down processes like predation, and bottom-up influences such as

moisture, are not temporally and spatially fixed, and will vary across both dimensions.

Further research is needed on the relative influences of sympatric terrestrial salamanders and other litter herpetofauna on the detrital food web and on each other, as they relate to environmental factors and litter retention. As the litter herpetofauna continue to respond to the effects of global climate change (see citations in *Introduction*) the need is urgent to better understand their ecological roles and how they may be altered by climate change. Only by increasing our understanding of these trophic linkages can we enhance our ability to manage forest ecosystems to maintain their vital ecological services and mitigate the adverse effects of anthropogenic changes.

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SUPPLEMENTAL MATERIAL

SUPPLEMENT

Raw invertebrate density data (count/g of litter) for all invertebrates encountered in soil samples on control and treatment plots during the time period of the study (2007–2009) separated by year (Year 1, Year 2), treatment of plot (C, T), and time interval sampled (T0–T5) for further analysis ([Ecological Archives C005-002-S1](#)).